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TRICHOMES OF THE ROOT IN VASCULAR CRYPTOGAMS AND ANGIOSPERMS.

By Robert Greenleaf Leavitt, A. M.

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No. 7.—TRICHOMES OF THE ROOT IN VASCULAR CRYPTOGAMS AND ANGIOSPERMS.[1]

BY ROBERT GREENLEAF LEAVITT, A. M.

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TWO CLASSES OF RADICAL TRICHOMES.

THE trichomes which arise in the superficial layer of the root of vascular plants as organs of absorption are of two types. Trichomes of one kind result from a differentiation of the meristematic cells of the young epidermis near the apex of the root; those of the other class have a simpler origin. The more commonly recognized and less highly specialized type will be first described.

[1] Contributions from the Ames botanical laboratory, no. 2.

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The First Type.

Trichomes of the first type are characteristic of the Dicotyledons, of some divisions of the Monocotyledons, and of the Filices. In these groups, as a rule, any cell of the piliferous layer may, at a certain stage in the development of the tissue, acquire the character of a trichome[1] by putting out a hair. All the cells over considerable areas may be piliferous, or only a part of them, determined apparently by chance. From the appearance of the cells of the young epidermis it is not possible to predict which ones are to become trichomes. Below the region of the youngest hairs there is no visible specialization or predetermination of the future trichomic cells. Every cell, we may suppose, is a potential trichome. The actual fate of any cell, whether it shall be that of a trichome or of an atrichomic element, is first to be ascertained in the young fixed tissue, after the cells have undergone a considerable extension, and after cell division has altogether ceased. The first indication of trichomic development is the appearance of a papilla, usually near the lower or distal end of the epidermal cell, that is, near the end lying toward the apex of the root.

Distribution of the first type in vascular Cryptogams and Angiosperms.— The following groups have been investigated with respect to the species named. The trichomes in these species are not predetermined in the nascent epidermis of the root, so far as can be seen.

Filices.

Hymenophyllaceae: *Trichomanes* sp.

Cyatheaceae: *Alsophila australis*, *A. Cooperi*, *Cibotium Schiedei*, *Cyathea insignis*, *C. medullaris*, *C. regalis*, *Dicksonia antarctica*, *D. davallioides*.

Polypodiaceae: *Adiantum aneitense*, *A. Capillus-Veneris*, *A. cuneatum*, *A. decorum*, *A. gracillimum*, *A. macrophyllum*, *A. Wie-*

[1] It seems necessary, in describing the structures under consideration, to use the word *trichome* for the whole cell, including the tube, or *hair*, or *root-hair*, and the basal portion imbedded in the epidermis, or *base*. The adjective *trichomic* and its opposite *atrichomic* have been coined for convenience in the present discussion.

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gandi, *A. Williamsii*, *Aspidium filix-mas*, *A. marginale*, *A. molle*, *A. trifoliatum*, *Asplenium angulare*, *A. bulbiferum*, *A. decussatum*, *A. Trichomanes*, *Blechnum brasiliense*, *B. occidentale*, *B. spicans*, *Cyrtomium* sp., *Gymnogramme sulphurea*, *Lomaria gibba*, *Microlepia hirta*, *Davallia fijiensis*, *Doodia rupestris*, *Nephrodium Shepardii*, *Nephrolepis bulbifera*, *N. davallioides*, *N. exaltata*, *Onoclea sensibilis*, *Pellaea hastata*, *Phegopteris polypodioides*, *Platycerium Alcicorne*, *Polypodium aureum*, *P. plectolepis*, *P. vulgare*, *Pteris aurata*, *P. cretica*, *P. pedata*, *P. serrulata*, *P. tremula*, *Scolopendrium vulgare*, *Woodsia obtusa*, *Woodwardia angustifolia*.

Osmundaceae: *Osmunda regalis*.

Marattiaceae: *Angiopteris evecta*, *Marattia alata*.

In *Ophioglossum vulgatum* and *Botrychium ternatum* (the only members of the Ophioglossaceae the roots of which were seen) no trichomes could be found.

The available species of the family Schizaeaceae were exceptional amongst the Filices examined in bearing trichomes of the second type. This case will be described below.

Hydropterideae.

Marsiliaceae: *Marsilia quadrifolia*, *M.* (*uncinata* ?).

In Azolla, the epidermis of the root has a somewhat complicated development, which is fully described below. Salvinia is without roots, if we except the transitory root of the sporeling, which I have not seen.

Monocotyledons.

In a large number of Monocotyledons the hairs are borne by special cells predetermined at an early stage, in the manner to be described below. The Liliiflorae, however, with but slight exception, the Spadiciflorae in the main, and numerous examples from other subdivisions of the Monocotyledons, present trichomes of the first type only. The species in which I have determined this to be the case are the following: —

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Glumiflorae.

Gramineae: *Brachypodium distachyon, Coix agrestis, C. lachryma, Eleusine corneana, Oryza sativa, Sporobolus airoides, S. cryptandrus.*

About 50 species of grasses were examined. Only the seven named were assigned to the class in which they are here put; and in several of these there was much doubt, and the determination was made provisionally. This matter will be further discussed below under Gramineae (p. 296).

Spadiciflorae.

Palmae. Of the palms examined only one had root-hairs. This was *Oreodoxa regia.* On the roots of seedlings a few hairs were found. They come from ordinary elongated epidermal cells. Gillain has examined the roots of many Palmae. The epidermis was one of the parts to which special attention was paid. In summarizing the results of this study of thirty-five species of palms he says of the epidermis: "It is retained only on the smaller parts of the roots, and then shows elongated cells, whose outer membrane is more or less strongly cuticularized. Only in *Trachycarpus excelsus* are hair formations and papillae present, such as Mohl has reported for *Diplothemium maritimum.*" [1]

Cyclanthaceae: *Carludovica atrovirens.*

Typhaceae: *Sparganium* sp., *Typha latifolia.*

Araceae: *Aglaonema picta, Anthurium Dechardi, A. magnificum, Arisaema triphyllum, Caladium esculentum, Dieffenbachia picta, Zantedeschia aethiopica.*

Liliiflorae.

Liliaceae: *Allium narcissiflorum, A. cepa, Anthericum Bernarnii, Asparagus plumosus, A. truophinus, Brodiaea congesta,*

[1] Gillain, G.: Beiträge zur anatomie der palmen- u. pandanaceen-wurzeln. Bot. centralb., **83**: 337 (1900).

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Dianella coerulea, *D. revoluta*, *Funkia ovata*, *Hyacinthus amethystinus*, *Lilium longiflorum*, *L. speciosum*, *Muscari Argaei*, *Xanthorrhoea arborea*, *Xerotes longifolia*.

Convallariaceae: *Aspidistra lurida*, *Cordyline stricta*, *Dracaena nutans*, *D.* hybrid, *Polygonatum biflorum*, *Yucca angustifolia*.

Amaryllidaceae: *Amaryllis amethystinus*, *Eucharis amazonica*, *Hypoxis erecta*, *Leucojum autumnale*, *Pancratium ovatum*.

Bromeliaceae: *Billbergia Leopoldii*, *B. Quesneliana*, *Nidularium argenteum*, *Tillandsia Lindenii*.

Iridaceae: *Freesia refracta*, *Iris Histrio*, *I. pseudacorus*, *Ixia* sp., *Moraea Robinsoniana*, *Sisyrinchium atlanticum*, *Watsonia Ardernei*.

The tegumentary tissues of the root were carefully examined and described by Juel for a large number of the Liliiflorae representing 42 genera. He makes no mention of specialized hair-cells in this group, although he noted several instances in other groups. This negative evidence is in agreement with my own observations. In the Liliiflorae in general the trichomes are of the unspecialized type.

Gynandrae.

The trichomes are sometimes predetermined, as in *Pogonia ophioglossoides* and other species mentioned below; but in many and probably in most of the Orchidaceae, any cell of the external layer may put out a root-hair as in *Goodyera tesselata*, *Liparis Loeselii*, *Odontoglossum luteo-purpureum*, *Selenipedium Sedenii*, *Vanda tricolor*, and *Vanilla planifolia*. In the Orchidaceae generally the tegumentary apparatus is highly modified. Of especial interest in connection with the occurrence of trichoblasts in several terrestrial species, is the character of the exodermal layer in the species the roots of which are provided with a velamen. The exoderm as constituted in these members of the group will be considered in another place.

Dicotyledons.

The Dicotyledons, with the exception of a single aberrant group, the Nymphaeaceae, to be discussed later, agree among themselves in

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the character of the epidermis of the root. The cells composing the superficial tissue in any given root are of generally uniform appearance in the younger stages. Root-hairs arise indiscriminately from all or any of the cells, after cell division has ceased and the cells have elongated. While the structural peculiarities to be found in Brasenia, Cabomba, Nuphar, and Nymphaea are probably attributable indirectly to the aquatic habit, it is instructive to find that aside from the genera named, none of the numerous aquatic Dicotyledons studied exhibits the same modifications.

The species which have been examined, arranged under the families to which they belong, are as follows: —

Casuariniflorae: *Casuarina equisetifolia.*
Urticiflorae: *Urtica dioica, Cannabis sativa.*
Polygoniflorae: *Peperomia* sp., *Polygonum Muhlenbergii, Rumex Acetosella.*
Curvembryae: *Beta vulgaris, Buda marina, Dianthus Caryophyllus, Salicornia herbacea, Spinacea oleracea, Sueda linearis.*
Polycarpicae: *Ranunculus aquatilis* var. *trichophyllus.*
Rhoeadinae: *Cardamine hirsuta, Nasturtium officinale, Papaver* sp.
Cistiflorae: *Drosera rotundifolia, D. intermedia, Elatine americana, Sarracenia* hybrid, *Viola blanda, V. primulaefolia.*
Gruinales: *Linum flavum, Oxalis* sp.
Tricoccae: *Callitriche verna, Euphorbia Poinsettia.*
Aesculinae: *Acer saccharinum.*
Frangulinae: *Vitis* sp.
Thymelaeinae: *Grevillea* sp.
Saxifraginae: *Bryophyllum calycinum, Chrysosplenium americanum.*
Rosiflorae: *Rubus* sp., *Spiraea astilbeoides.*
Leguminosae: *Phaseolus vulgaris.*
Passiflorinae: *Begonia Rex, B. metallica.*
Myrtiflorae: *Ludwigia Mullertii, Lythrum Salicaria, Myriophyllum ambiguum, Proserpinaca palustris, P. pectinacea.*
Umbelliflorae: *Daucus Carota, Cicuta* sp.
Hysterophyta: *Aristolochia elegans.*
Primulinae: *Lysimachia stricta.*
Personatae: *Pinguicula lutea, Mimulus ringens, Strobilanthes Dyerianus, Veronica scutellata.*

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Nuculiferae: *Coleus* sp., *Myosotis palustris*, *Scutellaria lateriflora*.
Contortae: *Limnanthemum nymphaeoides*, *L.* sp., *Menyanthes trifoliata*, *Sabbatia* sp.
Campanulinae: *Lobelia Dortmanna*, *L. cardinalis*.
Synandrae: *Aster* sp.

Trichomes of the Second Type.

Trichomes of the second type originate early in the development of the piliferous layer as specialized elements. Only cells which are predetermined for the purpose in the young epidermis bear root-hairs. Differentiation begins with an act of division taking place in a cell of the embryonic tissue near the growing point. The nucleus assumes a position away from the center, toward one end of the cell (pl. 17, fig. 31, T). After the completion of nuclear division the new transverse wall cuts off a segment which in many cases comprises no more than a fourth or even a fifth of the original cell. The segmenting wall is often curved, whether viewed in longisection or tangentially (pl. 16, figs. 20, 21). It is often oblique, so that the segment in question appears more or less wedge-shaped. The new cell is at once seen to differ from its larger sister cell in its optical and staining qualities. In the living state the shorter cell appears more highly refractive. Its cytoplasm and nucleus stain more deeply in prepared sections.

By the division of the original epidermal cell, therefore, there is effected a differentiation which is manifested immediately in the size, shape, and contents of the two resulting cells. The subsequent development of these two elements fulfils the expectation which may be formed from their initial differences, the anticipation that they will play very dissimilar parts, structurally and functionally, in the mature epidermis. The larger cell of the pair elongates considerably, sometimes enormously. In many cases it habitually divides transversely, once or several times (pl. 16, fig. 9). It is non-piliferous. The shorter and denser cell, on the contrary, elongates but little as a rule. It very seldom divides transversely. Very soon, in the zone of increasing elongation of the young root trunk, it becomes papillate, and later piliferous (pl. 16, fig. 1–3).

The shorter, often wedge-shaped, often lenticular, and generally denser segments resulting from differentiating divisions in the

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embryonic epidermis are thus the primordia of the trichomes. For the sake of brevity I shall apply to them in this paper a distinctive term, and shall speak of them as *trichoblasts*.

The distance from the apex at which trichoblasts begin to appear varies with the size of the root and the rapidity of growth. I have often found them forming within 10 or 12 cells of the growing point, in the case of rootlets fine enough to be studied without sectioning (pl. 18, fig. 71).

In the greater number of cases, the trichoblast is cut from the upper or proximal (basal) end of the mother cell, *e. g.*, *Aneimia adiantifolia* (pl. 16, fig. 1), Isoetes, Selaginella, Lycopodium, Limnocharis, Commelina, Nymphaea; in some cases, however, from the lower, *e. g.*, Azolla, Juncus, Luzula, Scirpus, Alopecurus (pl. 18, fig. 65).

The relative sizes of the trichoblast and the atrichomic sister cell vary in different groups of plants, and to some extent even in the same species. The disparity may be slight, as in many Gramineae (pl. 18, fig. 68).

In Azolla it would appear from the ascertained position of the newly formed daughter nuclei and of the connecting fibers that the axis of the mitotic figure, in the mitosis giving rise to the trichoblast, is inclined (pl. 16, fig. 5). In Azolla, Lycopodium, and probably in other cases, the obliquity of the segmenting wall is fixed in the process of cell division. It is not due to subsequent changes in the forms of the cells.

In most species of Lycopodium the division wall does not extend to the inner face of the mother cell, but abuts internally upon the proximal end wall of the cell (pl. 16, fig. 20). The trichoblast therefore has a sharp inner edge, and appears like a wedge inserted between two adjacent epidermal cells. It was mainly this peculiarity which drew the attention of the earlier anatomists to the specialized character of the hair-cells in Lycopodium, while the no less specialized structures to be found in so many groups have escaped general notice. Nägeli and Leitgeb explained the origin of the trichomes in Lycopodium (see note under Lycopodium below). They neglected the almost equally striking trichoblastic elements of the young root of Equisetum, the development of which root they described in detail. De Bary (Comparative anatomy, 1884, p. 60) says: "Only in Lycopodium can special hair-cells be distin-

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guished from the other epidermal cells of the root." A few notices of special hair-cells, observed in several plants, but without statements as to their origin, are to be found. The distribution of these structures in vascular plants seems not heretofore to have been considered.

In some plants the trichoblast not infrequently undergoes transverse division. Two or more trichomes may then stand in succession in the same longitudinal cell series. In a few cases the trichoblast frequently or regularly divides longitudinally once (some species of Lycopodium, Luzula, Anigozanthos), or twice successively (Lycopodium, Lachnocaulon). In this way groups of 2, 3, or 4 trichomes, standing side by side, are formed (pl. 16, fig. 22; pl. 17, fig. 55; pl. 18, figs. 75, 84) intercalated between the ends of neighboring non-piliferous cells. But in general, trichoblasts and the resulting trichomes stand singly amongst the other elements of the superficial layer.

The atrichomic segment may or may not divide. For example, in Lycopodium the non-piliferous cells never divide so far as I have seen. In the maturer tissue, therefore, the trichomes occur regularly alternating with elongated hairless cells. In some groups, however, the latter at an early stage divide transversely and the transverse divisions are made in an orderly manner. In these cases the trichomes occur at regular intervals in the longitudinal rows, interspaced as a rule by a given number of elongated cells. The most pronounced instance observed is that of Azolla, in which the uniformity of the divisions in different longitudinal rows often gives a zonal arrangement of the trichomes. The figures of Isoetes may also be referred to in this connection (pl. 17, fig. 23–26).

Speaking generally of those groups and species in which trichomes of the second type occur, the formation of trichoblasts is not an inevitable event in the development of the epidermis. They may be more or less extensively intermitted for a time. They seem to be called out by some stimulus in the substratum. When the stimulus is inoperative the trichoblasts are not formed. In this event the roots are hairless. Thus Elodea is mentioned by De Bary as being destitute of root-hairs. Yet under proper conditions trichomes are produced. They are of trichoblastic origin. Nymphaea, also, is often given in the textbooks as a plant without root-hairs. But these organs may be found in abundance, borne by differentiated cells, on roots rapidly growing in soil rich in nutritive matter.

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The trichoblast, even when formed, does not always become a trichome. It may remain short without putting out a hair, or it may become somewhat elongated and resemble an atrichomic cell. A singular outcome is to be seen in Nymphaea, in which trichoblasts which are not to be piliferous become suppressed and are overlaid by the conjoined ends of the elongated cells standing next above and below in the row.

The base of the mature trichome is characteristically short when compared with the adjacent non-piliferous cells. It is often strongly wedge-shaped (Aneimia, Equisetum, *Selaginella rupestris*, Lycopodium, Sagittaria, Naias). Its inner wall is often pushed out under the extremities of the contiguous cells of the same row, as in many of the Helobieae, notably in Naias (pl. 17, fig. 42). In Naias, Potamogeton, and Cymodocea, Sauvageau has observed that the piliferous cells persist after the other external cells have fallen away. The base of the trichome sometimes presses in upon and displaces the underlying cortical cells, as in *Limnobium Spongia* (pl. 17, figs. 49, 51).

The nucleus, along with much protoplasmic matter, often lies in the basal part of the cell (pl. 17, figs. 48, 51). This is in contrast to the condition prevailing in trichomes of the first type, where, after the growth of the hair is completed, the nucleus takes up a position about midway of the tube, as a lenticular body adherent to the wall. The nucleus of the trichoblast may be very much larger than the nucleus of the surrounding cells, as in *Limnobium Spongia* (pl. 17, fig. 49). The walls of hair-cells of this type are often darker colored than the walls of the non-piliferous cells.

In those species in which the trichomes are of the specialized character described above, the epidermis of the root is thus composed of two very different elements. The development of this complex integument may be described as follows. Beginning with the parts nearest the apex, we have *first*, a short zone of cells undergoing equating divisions; *second*, a region in which by differentiating divisions the trichoblasts are cut off in a generally acropetal succession; *third*, a zone in which the atrichomic cells elongate and divide transversely (though division may be characteristically absent); in this zone the trichoblasts may become papillate; finally a *fourth* region, where, with the completion of division, the tissues of the root rapidly elongate, the root-hairs grow to their full size, and the layer becomes fixed.

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It is noteworthy that when trichoblasts are formed the other epidermal cells do not put out hairs. In species characteristically trichoblast-bearing, even when these organs are absent no root-hairs appear.

It would seem that in certain groups and species of plants the capability of receiving and responding to the stimulus which initiates the formation of root-hairs is strictly localized in a portion of the dermatogen very near the extremity of the root trunk. Could we follow the protoplasmic movements within the cells of this region, the first visible response would probably be the transference of the nucleus from its usual central position to a station nearer one of the end walls. The first sign of activity manifest upon an inspection of the living tissues, however, is the existence of new transverse walls peculiarly situated, as already described. These operations in the meristematic zone, with their proper sequel in the further development of the trichoblasts, appear to be the only mode in which large numbers of plants are able to react structurally to the stimuli which call forth root-hairs.

Distribution of Trichomes of the Second Type in Vascular Cryptogams and Angiosperms.

General distribution. — Hair-cells of trichoblastic origin are found in the Schizaeaceae amongst Filices, in Equisetum, in Azolla, in Lycopodium and Phylloglossum, in Isoetes, and in Selaginella; in all the Helobieae examined, in nearly all the Glumiflorae examined, in some of the Spadiciflorae, in the Enantioblastae, in one genus of the Liliiflorae, in several orders of Scitamineae, in several terrestrial orchids among the Gynandrae; and finally in the Nymphaeaceae, where their occurrence is associated with an epidermal arrangement anomalous amongst Dicotyledons.

Distribution of the second type; description of examples in the larger groups. — The origin, development, and anatomical characters of trichomes of this type are now to be described in detail in connection with the groups and species in which they have been found to occur, either by myself or by observers who will be named. Species given without comment are species in which the hair-cells are predetermined, but of which nothing further need be said.

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Filices.

In most of the true ferns, the roots of which were studied, the hair-cells are ordinary epidermal cells. A list of the species is given above. The following proved exceptional:

Schizaeaceae: *Aneimia adiantifolia*, *A. fraxinifolia*, *Lygodium dichotomum*.

Aneimia adiantifolia (pl. 16, fig. 1–3). — In sections of a certain actively growing root, the cap extends over about 40 cells of the epidermis, counting in a single longitudinal cell series. At its edge the hair-cells appear in longisection as short, somewhat wedge-shaped, dark cells, whose outer walls project somewhat from the general surface of the epidermis. Following the layer toward the apex, a series of cell-pairs can be seen, ending with the 22d cell from the growing point. Here by a recent transverse division the first of the cell-pairs has been formed from a mother cell, the distal member being the longer in the ratio of 2: 1. The proximal, shorter, and very slightly wedge-shaped cell is the trichoblast.

A few cells back of the root-cap, the atrichomic cells are seen in a much elongated condition (pl. 16, fig. 2). The trichoblasts have become elongated to a less degree, and are broadly triangular in outline. As they develop, the hairs are directed obliquely toward the root tip. The base of the trichome is wedge-shaped.

Only the three species of the Schizaeaceae named above were available for examination. They agree very closely in the appearance of their trichomes.

Hydropterideae.

Azolla caroliniana and *A. filiculoides* agree in the origin and character of their root-hairs.

The root is provided with a root-cap of two cell layers. The outer is much the shorter and except at the apex is separate from the inner. The latter forms at first a close covering for the trunk. The initials of the trichomes arise within a belt of actively dividing cells, lying immediately under the inner root-cap, not far from the apex, at an actual distance varying with the rate of growth of the terminal region (pl. 16, fig. 4, T). The division is oblique. Only the final stage

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of nuclear division was obtained in sections. At this stage, however, the obliquity of the new cell wall is already determined (pl. 16, fig. 5, d). Of the two more or less wedge-shaped elements so formed, the lower and slightly larger one is the hair initial or trichoblast. As the root reaches the limit of its development, the hair-forming impulse travels downward until the apical cell itself is split into several parts, each piliferous.

The trichoblast never elongates much in a direction parallel to the length of the root. It may divide transversely once, as in rare instances two trichomes are found standing in succession. The tube, which presently begins to grow out, turns toward the root apex (pl. 16, figs. 7, 8, 9). As the hairs lengthen they at first lie appressed to the root and may be seen confined by the inner cap, which is now pushed away from the root trunk. The whole cap structure is finally thrown off through the growth of the lower hairs, and the hairs themselves stand out strongly (pl. 16, fig. 11). Their bases retain the wedge form of the original hair initial (pl. 16, fig. 10).

Soon after their organization, the hair initials are to be distinguished from the cells with which they alternate by their contents no less than by configuration, since they are more richly supplied with protoplasm (pl. 16, fig. 6). In the younger portion of the root the transverse divisions of the piliferous layer are very uniform. The cells therefore stand in fairly regular and continuous zones. This arrangement is manifested by the young hairs (pl. 16, fig. 8).

The lesser wedge-shaped cell produced simultaneously with the hair initial elongates and soon divides transversely (pl. 16, figs. 7, 9) once, twice, and often three times. The trichomes in each longitudinal cell row thus become separated by two, four, or eight cells. The intervening cells may be six, however. The number of divisions in neighboring rows may be different; and through the resulting displacements the original regularity of the hair zones is destroyed (pl. 16, fig. 11).

EQUISETINAE.

Equisetum arvense (pl. 16, fig. 12–15).— The trichoblast may be seen under the root-cap in the longisection of the root, as narrow, proximal segments of lately divided epidermal cells (pl. 16, fig. 12), the wall of division often being curved toward the apex of the root,

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as it meets the outer wall of the mother cell. The somewhat older trichoblasts are wedge-shaped (pl. 16, fig. 13), and this form is seen in the trichome (pl. 16, fig. 15). In superficial view, at a point immediately back of the cap, the trichoblasts appear strongly convex laterally and somewhat wider than the atrichomic cells (pl. 16, fig. 14). At times the piliferous and non-piliferous elements alternate regularly; at other times the trichomes are found scattered irregularly. The hair is at first directed obliquely toward the apex of the root.

All the species seen agree closely in the character of their trichomes. The following were examined: *Equisetum arvense*, *E. debile*, *E. diffusum*, *E. hyemale*, *E. limosum*, *E. litorale*, *E. ramosissimum*, *E. scirpoides*, *E. variegatum*.

Lycopodinae.

Lycopodium.— Nägeli and Leitgeb[1] describe the origin of the trichomes in *Lycopodium clavatum*. From this account, which is illustrated by diagrammatic figures, we learn that the trichomes first appear under the root-cap in the form of wedge-shaped portions cut off by oblique walls from the basal half of the young epidermal cells. These wedge-shaped cells divide from one to three times, by walls at right angles to the oblique wall, to form from 2 to 4 adjacent cells, each of which grows out into a root-hair, while the remaining part of the original epidermal cell at once elongates. Sometimes only a corner of the epidermal cell is cut off, in which case but one hair is formed.

The same history is to be given for several native species of Lycopodium which I have examined; *viz.*, for *L. annotinum*, *L. dendroideum*, *L. lucidulum*, *L. obscurum*, *L. sabinaefolium*, and *L. sitchense*. *Lycopodium inundatum*, however, departs from the usual type. This species and *L. lucidulum* are now to be described in detail, with the reproduction of drawings from nature.

Lycopodium inundatum (pl. 16, fig. 16–19).— In the development of the epidermis the differentiation of the trichomes begins within a very short distance of the apex. In a typical case the first

[1] Nägeli & Leitgeb: Entstehung und wachsthum der wurzeln. C. Nägeli's Beiträge zur wissenschaftlichen botanik, **4** (1868).

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differentiating division was observed to have taken place, in a certain row, in the 12th cell from the growing point, under the root-cap (pl. 16, fig. 16). The cell was tabular, half as long as high (radially). A straight transverse dividing wall had been laid down separating the original cell into two almost equal parts, representing the first stages of the atrichomic and trichomic components of the epidermis. That the two segments are often nearly equal was ascertained. As a rule, however, the basal or proximal segment is the shorter. In general, the division wall is curved toward the root apex as it approaches the exterior. Not infrequently its position is somewhat oblique, and the resulting segments are therefore somewhat wedge-shaped.

The proximal segment is the more highly refractive in appearance, and a short time after its formation its contents become dark and granular. As a rule it elongates little with the growth of the tissue. This cell is the trichoblast. The distal cell of the pair very soon becomes turgid and convex, pressing in upon its sister cell, and in contrast to the latter, rapidly elongates, ultimately attaining to many times its original length. The epidermis thus consists of two kinds of cells, not remarkably unlike at the moment of their derivation from common mother cells, but exhibiting, even before they have escaped from under the short root-cap, a strong contrast in size, form, and contents.

At a little distance back of the root-cap, the trichoblasts develop into trichomes. The incipient hair, as a papilla in which the nucleus often lies, at first turns towards the root apex (pl. 16, fig. 17). The base of the mature trichome is often much compressed between the convex ends of the adjacent elongated cells, but spreads out where it abuts upon the subjacent cortical layer, as well as externally, at the foot of the tube (pl. 16, figs. 17, 18).

The trichoblast commonly does not divide longitudinally, although instances of such division may be found. The hairs are therefore borne singly, as a rule. When the trichome is viewed in tangential section it is seen that the hair emerges somewhat laterally. The hair occupies the position that one of the two hairs would hold, had the trichoblast divided longitudinally for the production of a pair of trichomes. This peculiarity is interesting, for it is found in other species of Lycopodium when the trichoblast remains undivided.

The lateral position of the hair upon the trichome base is charac-

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teristic of some other groups, for example, some Monocotyledons, where it occurs along with occasional longitudinal splitting of the trichoblasts (pl. 18, fig. 86).

A single case of transverse division of a trichoblast was seen. The atrichomic cells seem rarely, if ever, to divide transversely after the trichome initials appear. The cutting off of trichoblasts may be intermitted. Generally, however, the trichomes are produced very abundantly.

Lycopodium lucidulum (pl. 16, fig. 20–22). — The earliest rudiments of the trichomes lie close to the apex, under the root-cap. The transverse wall, separating the newly formed trichoblast from the atrichomic sister segment of the original tabular epidermal cell, is oblique and curved. Beginning near the inner edge of the proximal end wall of the mother cell, this membrane of division runs outward at an acute angle with that wall, toward the external face of the mother cell. At length it curves toward the root apex, and as seen in longisection meets the outer wall usually a little forward of the middle point (pl. 16, fig. 20, T). In tangential section, also, the new wall is curved, with the convexity toward the root apex (pl. 16, fig. 21).

The lenticular, wedge-shaped, proximal segment thus cut off is from the first distinguished by relatively dense contents. This cell is the trichoblast. As the elements of the layer increase in radial and longitudinal dimensions, the atrichomic cells outstrip the trichoblasts. The latter soon reach full size, while the intervening cells continue to elongate. Immediately back of the root-cap the outer face of the trichoblast becomes protuberant. The further extension of this wall in tubular fashion, in adaptation to the absorptive function of the cell, gives rise to a hair which at first is inclined somewhat forward, toward the root apex (as in *Lycopodium inundatum*, Equisetum, and Azolla).

Sooner or later the trichoblast generally divides longitudinally once (pl. 16, fig. 22); or, less frequently in this species, twice successively. The trichomes are therefore to be found generally side by side in pairs, or more rarely in groups of four. If no longitudinal splitting occurs, the single hair arises aside from the median position, as in *L. inundatum*. Not infrequently in the material examined, cases were found where two trichoblasts had been formed successively in the row.

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The fully formed trichome consists of a long and slender hair, and a sharply wedge-shaped base, intruded between two elongated epidermal cells and reaching usually somewhat more than half way to the inner plane of these cells.

Phylloglossum. — Roots of *Phylloglossum Drummondii* from dried specimens treated with caustic potash showed the structure of the older epidermis well. Long hairless cells and short piliferous cells alternate in the longitudinal rows, as in Lycopodium. The root tips were not seen.

Isoetes (pl. 17, fig. 23–27). — In Isoetes the production of trichomes is initiated by the formation of trichoblasts in the embryonic region, near the apex of the root. The fact that the trichomes of the root of Isoetes are predetermined was stated by H. Bruchmann, in his paper, Ueber anlage und wachsthum der wurzeln von Lycopodium und Isoetes (Jenaische zeitsch., **8**: 522, 1874).

The trichoblast may arise from the simple bipartition of a cell. In this case the dividing cell is cut, in general unequally, by a transverse wall perpendicular to the outer and inner faces. The upper or proximal segment becomes the trichoblast. It is readily distinguished from the surrounding cells in the living root by the somewhat greater refractive power of its contents.

Generally, however, the process is somewhat more complicated. As a rule in the species examined, especially in freshly growing roots, the trichoblast is the proximal member of a group of four cells produced from an original unit by two successive divisions (pl. 17, fig. 23). That the trichoblast is from the moment of its inception a cell of specialized character is manifested by the fact that, while the second division gives in the lower half of the original cell two elements of the same size and appearance, in the upper half it results in unequal and dissimilar cells, of which the smaller and denser is the trichoblast (pl. 17, fig. 23, T; fig. 24).

The atrichomic cells of the group may, and generally do, remain undivided. Then the trichomes ultimately stand in the mature epidermis at set intervals, being separated in the rows by 3 non-piliferous cells (pl. 17, figs. 25, 26). But sometimes the intervening cells are increased by further division so that the trichomes are separated by 4 or more cells in the row.

In rapidly growing roots the trichoblasts become papillate immediately back of the embryonic area. At maturity the trichomic

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cells are considerably shorter than their atrichomic neighbors (pl. 17, fig. 27). The fully grown tube is long and slender.

Under certain conditions of growth or environment of the root, no trichoblasts are produced. In such cases the roots remain without root-hairs.

The following species were examined: *Isoetes azorica*, *I. Bolanderi*, *I. Butleri*, *I. canadensis*, *I. Eatoni*, *I. echinospora Brauii*, *I. Echinospora muricata*, *I. Engelmanni*, *I. foveolata*, *I. Howellii*, *I. hystrix*, *I. Kirkii*, *I. macrospora*, *I. melanopoda*, *I. melanospora*, *I. Nuttallii*, *I. Piperi*, *I. riparia*, *I. saccharata*, *I. Tuckermanni*.

Selaginella (pl. 17, fig. 28–30). — The differentiation of the trichomes, in their earlier as well as their later stages, is very marked in *S. rupestris*. In the fixed tissue of the epidermis the short hair-cells often alternate regularly with elongated hairless cells. The bases are a little wider than other cells of the row, and the hair is often borne somewhat laterally. In longisection the bases are characteristically more or less wedge-shaped (pl. 17, fig. 29). The hair is sometimes branched.

The hair initials are determined in the meristematic tissue. In figure 28 (plate 17) the origin of the trichoblast is shown at T. An epidermal cell at the edge of the root cap has been divided near its proximal end. The narrower tabular segment, comprising about one third of the original cell, is the trichoblast. Both cells immediately elongate, decreasing meantime in radial diameter. In the tissue immediately succeeding them the short, dense trichoblasts stand out prominently amongst the more transparent elements.

In most species of Selaginella examined the roots were poorly supplied with root-hairs. Neither a regular alternation of trichomic and atrichomic cells, nor the existence of cells in the young epidermis destined to produce hairs could be demonstrated. The hairs stood singly. All the cells were relatively short, but nothing was seen to indicate that the origin of the trichomes is different from that in other species where they are plainly of the specialized type, *e. g.*, *S. denticulata* (pl. 17, fig. 30), *S. Martensii*, and *S. viticulosa*.

Helobieae.

Throughout this group trichoblastic hair-cells are characteristic. They are conspicuously different from the generally much elongated

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atrichomic elements, and have not escaped observation. The degree to which they characterize the group has apparently not been understood, however, and their origin has not been determined by the observers who have described the hair-cells as being peculiar. The notes of several investigators, quoted below, represent practically the entire literature of the subject, as far as Monocotyledons are concerned. Species named without comment have been determined by me to possess the characteristic trichomes of the group. But, before the investigated species are enumerated, two typical cases may be described with some particularity.

Limnocharis emarginata (pl. 17, fig. 31–33).— If a freshly growing root be sectioned longitudinally, the fundaments of the trichomes may be seen, let us say, within twenty cells of the apex. In a particular section examined, the 18th and 19th cells in a certain row were tabular in form, with a radial height exceeding twice their individual lengths. The 20th cell had lengthened and become nearly isodiametric. The nucleus, in the last phases of division, was lying near the proximal end of the cell, preparation having thus been made for the cutting off of a short proximal segment, the trichoblast (pl. 17, fig. 31, T). From this point backward, a succession of alternating denser and less dense, shorter and longer cells could be followed. The trichoblasts at first are tabular. A short distance back of the edge of the root-cap, the atrichomic cells, which were not often divided, had become very greatly elongated, the trichomic cells relatively very little elongated (pl. 17, figs. 31, 32). The base of the matured trichome is longest where it meets the underlying cortex, and narrows to the foot of the hair (pl. 17, fig. 33). Base and hair are well supplied with protoplasm. The nucleus, which is not extraordinary in size but stains more deeply than the nuclei of the atrichomic cells, lies in the base of the trichome, or less frequently a short distance up in the tube.

Sagittaria Eatoni (pl. 17, figs. 43, 44).— The origin of the trichoblasts may be studied in the finer rootlets without sectioning. Before differentiation the young epidermal cells, near the apex of the root, become nearly isodiametric. In each mother cell a segment occupying from one fourth to one third of the space at the proximal end is cut off by a straight transverse wall (pl. 17, figs. 43, 44). In tangential section the trichoblastic segment may be slightly lenticular. The subsequent development of this cell resembles that

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given for the hair-cell of *Limnocharis emarginata*. Trichomes and elongated cells often alternate with entire regularity. The prismatic non-piliferous cell may, however, divide transversely once or twice. The trichoblast may mature as a hairless short cell. Trichoblasts may be absent for a time under conditions, as we may suppose, not calling for absorptive activity on the part of the root.

The following species belonging to the Helobieae have been examined. The hair-cells arise as trichoblasts.

Juncaginaceae: *Triglochin maritima* (pl. 17, fig. 34). This example was also noted by Juel (*l. c.*).

Potamogetonaceae: several native species of Potamogeton were investigated. Trichomes are abundant, with bases only one fifth or one sixth the length of the non-piliferous cell. The walls are often dark colored. Sauvageau[1] notes the peculiarities of the trichomes in the European species seen by him and says that those superficial cells which bear the hairs persist longer than their congeners. *Ruppia maritima* (pl. 17, fig. 35). *Zannichellia palustris* (pl. 17, fig. 36). *Zostera marina.* Trichoblasts are formed. Sauvageau, in the paper above cited observes that the peculiar piliferous cells persist after the fall of the other epidermal cells.

Cymodoceae: Sauvageau has called attention to a differentiation of piliferous and non-piliferous cells in the epidermis in this group.[2] The structure is very much like that observed by him in Naias. "A longisection of the tip of the root shows that at first the cells of the piliferous layer are of equal size, but they are soon differentiated, on the one hand into cells which remain narrow (short), become conical and develop into hairs, and on the other hand into cells which follow the elongation of the root and do not produce hairs." The latter soon fall off, while the trichomes persist for a longer time.

Aponogetonaceae: *Aponogeton distachyum*, *Aponogeton* (*Ouvirandra*) *fenestrale.*

Naiadaceae: *Naias gracillima* (pl. 17, fig. 37–40). The mature epidermis consists of exceedingly elongated cells — the ratio of

[1] Sauvageau: Journ. de bot., **3**: 169 (1889).

[2] Sauvageau: Sur la racine des Cymodoceae. Association française pour l'avancement des sciences, 20e session, p. 473 (1891).

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length to breadth was found in cases to be 27 : 1 — and, between their ends, the peculiar trichomes. The bases of the latter, with abundant granular protoplasm, push out under the cells standing next above and below, and press their inner walls into the adjacent cortical tissue. Early stages of the trichomes are shown in figure 37 to 40 (plate 17). The trichoblasts originate as short, proximal segments. In longisection they at first appear tabular, later conical, with expanded inner base. In tangential section they appear lenticular, and narrower than the atrichomic cells. *Naias flexilis* (pl. 17, figs. 41, 42) agrees with *N. gracillima*. *Naias major*, *N. minor*. The descriptions by Sauvageau show that the trichomes are of the same character as those of *N. flexilis*. The hairless cells ultimately fall away, leaving the hairs still standing in a living condition as shown by the contents.

Alismaceae: *Limnocharis emarginata*, *L. Humboldti*, *Alisma Plantago*, *A. ranunculoides* (Juel, *l. c.*), *Sagittaria Eatoni*, *S. lancifolia* (pl. 17, fig. 47), *S. montevidensis*, *S. natans*, *S. subulata* (pl. 17, figs. 45, 46), *S. variabilis*, *Lophotocarpus subulatus*.

Hydrocharitaceae: *Limnobium Spongia*. The root-hairs are extraordinarily large and long, from cells exceeding the neighboring cells in breadth and depth, in amount of protoplasm, and in the size of the nucleus (pl. 17, fig. 51). The appearance of the trichoblast near the edge of the root-cap, is shown by figure 49 (plate 17). *Stratiotes aloides* closely resembles the above species in respect to trichomes of the root. A description has been given by Kny. *Hydrocharis Morsus-ranae* and *Hydromystria stolonifera* are included in his account. "In the three species named root-hairs arise from only a small number of epidermal cells. Those cells which are destined to grow out [into hairs] lie scattered amongst the others without recognizable order."[1] Kny says that the hair fundaments are first produced where the root begins to penetrate the mud in the places where these plants grow. *Vallisneria spiralis* and *Elodea canadensis* show trichoblastic hair-cells.

[1] Kny, L.: Sitzungsb. d. bot. vereins d. prov. Brandenburg, 26 April, 1878, p. 48.

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Glumiflorae.

In Juncaceae, Cyperaceae, and many Gramineae, the specialized character of the trichomic cells is marked. In many members of the Gramineae the external differentiation of the hair-cells, though pronounced enough to be unmistakable, is not great. In a few species all distinction of trichomic and atrichomic cells seems to have been lost.

As illustrative of the Glumiflorae several species may be examined in some detail.

Alopecurus occidentalis.— The development of the epidermis may be traced in detail in rapidly growing rootlets. The cap is very small; the rootlets are transparent. Proceeding from the apex, and following a longitudinal cell row, the following sequence of elements was observed in a particular case. (1) Equal sided cells, as viewed in full face, 9 in number. These may divide transversely, or split longitudinally to institute new rows. (2) Cells wider in consequence of the growth of the root in circumference and shorter by reason of repeated transverse division, up to the 22d cell from the apex. (3) Cells in which trichoblastic segments have been formed, beginning with the 23d from the apex. A regular alternation of dissimilar cells — trichoblasts and their sister cells — now follows. In longisection the wall separating the sister cells of the same pair is inclined backward; the lower, slightly shorter and more refractive cell, the trichoblast, being thus a little wedge-shaped, with its thinner edge inward. (4) Trichoblasts alternating with two atrichomic cells, beginning after the 32d cell from the apex. The atrichomic cells in this region divide transversely (pl. 18, fig. 65). (5) Marked elongation of all the elements including the trichoblasts, which though throughout distinguishable in size and contents from the atrichomic elements, may nearly equal the latter. The hairs now appear. The evolution of the piliferous layer is complete.

Carex crinita.— The piliferous layer presents some differences of appearance in different roots of the same individual plant. On fine rootlets observed the cells were comparatively short. Even in these rootlets, however, the specialized nature of the trichomes and of the cells destined to become trichomes is evident. In a particular case, typical of the roots examined, the first transverse divisions pre-

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paratory to the formation of trichomic cells were observed about 12 cells from the apex. The cells immediately below — the next younger — were of uniform size and appearance. The divisions mentioned segmented the mother cells into two unequal parts in each instance, having lengths as 3 to 2. The distal segment was the shorter; this was the trichoblast. From this point backward a regular succession of cell-pairs was to be seen in which shorter and denser trichomic cells alternated with those of an opposite character (pl. 18, fig. 60). The series was followed up to the root-hairs, about 0.6 mm. from the end of the root. The ultimate lengths of the two sorts of epidermal cells were as 3 or 4 to 1. In larger roots the hairless cells were 6 or 7 times as long as the trichomes.

Luzula campestris.— The trichoblasts originate as short tabular segments, including the lower one third to two fifths of the original cell room. They are frequently divided after a short interval, either transversely or longitudinally (pl. 17, fig. 55). In the latter event two root-hairs are formed side by side, as in *Lycopodium lucidulum* and in *Anigozanthos pulcherrima*. The three species of *Luzula* which I have seen agree in the above particular. The incipient hair is inclined forward, as in several of the vascular Cryptogams already described.

In all species of Glumiflorae in which the matter has been accurately determined, the trichoblast comes into existence as a *distal* segment in the differentiating division.

I have examined the following species of the Glumiflorae and find the presence of predetermined hair-cells.

Juncaceae: *Juncus acuminatus*. The trichoblast is from the lower end of the mother cell. It often divides transversely so that 2 or even 3 trichomes may stand in succession (pl. 17, fig. 53). *Juncus arcticus*. The origin and superficial appearance of the trichoblasts is shown in figure 52 (plate 17). *Juncus glaucus*. The trichoblast is cut off distally. *Juncus marginatus*, *J. militaris*, and *J. tenuis*. *Luzula campestris*, *L. comosa*, *L. sudetica* (pl. 17, fig. 54–56).

Cyperaceae: *Carex albicans*, *C. conoidea*, *C. crinita*, *C. foenica* var. *sabulonum*, *C. Houghtonii*, *C. maritima*, *C. Muhlenbergii*, *C. muricata*, *C. pennsylvanica*, *C. Tuckermanii*, *Cyperus alternifolius* (pl. 18, figs. 58, 59), *C. filiformis*, *C. natalensis*, *C.*

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Nuttallii, *C. rivularis* (pl. 18, fig. 57, where the origin and transverse division of the trichoblast is seen). *Dulichium spathaceum*, *Eleocharis palustris*, *Eriophorum alpinum*, *Fimbristylis autumnalis*, *Hemicarpha subsquarrosa*, *Isolepis gracilis*, *Kilingia pumila*, *Rhynchospora fusca* (pl. 18, fig. 62), *Scirpus atrovirens*, *S. debilis*, *S. maritimus* (pl. 18, figs. 63, 64), *S. setaceus*.

Gramineae. The trichoblastic elements may be numerous, short in comparison with the other cells of the epidermis, and thus readily distinguished as in *Sorghum vulgare*, *Anthoxanthum odoratum*, *Panicum sanguinale*, and various species of Poa. On the other hand the origin of the hair-cells is often difficult to make out. The differentiating division results in two segments of about equal size, and of nearly similar contents. The atrichomic cell may subsequently divide. In the mature epidermis the trichomes and atrichomic cells do not differ much. Differentiation is less pronounced, and seems in reality to be passing away. In some members of the group, in fact, the entire epidermis may be piliferous; the habit of setting apart special cells for the bearing of root-hairs has been lost. *Oryza sativa* is one of the very few examples found in a large number of grasses examined in which the entire loss of the trichoblastic character was definitely ascertained. The following show specialized hair-cells: *Agrostis Steeveni*, *A. stolonifera*, *A. vulgaris*, *Alopecurus occidentalis*, *Andropogon nutans*, *Anthoxanthum odoratum*, *Asprella hystrix*, *Avena sterilis*, *Briza gracilis*, *Bromus asper*, *B. albidus*, *B. giganteus*, *B. purgans*, *B. Richardsoni*, *Calamagrostis hyperborea*, *C. montanensis*, *Chloris elegans*, *Deschampsia cæspitosa*, *Elymus virginicus*, *Festuca ampla*, *F. duriuscula*, *F. ovina*, *F. arundinacea* (pl. 18, fig. 68), *F. pratensis*, *Holcus lanatus*, *Hordeum nodosum*, *H. pusillum*, *Lolium italicum*, *Miscanthus candensatus*, *Panicum sanguinale*, *P. saccharatum*, *Pappaphorum Wrightii*, *Paspalum tenellum*, *Phalaris canadensis*, *P. paradoxa*, *Phleum asperum*, *Poa* sp., *P. laevigata*, *P. violacea* (pl. 18, fig. 69), *Polypogon monspeliensis*, *Puccinellia airoides*, *Sorghum vulgare*, *Sporobolus airoides*, *S. cryptandrus*.

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Spadiciflorae.

A list has already been given of the Spadiciflorae in which I have found the trichomes to be of the unspecialized type. In two cases I have found that the hair-cells are of the second type, *viz.*, in a hybrid seedling, *Anthurium Andreanum* × *A. ornatum*, and in *Monstera deliciosa*. Figure 70 (plate 18) shows the young trichomes of the root in the latter species. An alternation of hairless cells and trichomes with wedge-shaped bases is seen in longisection. The base of the trichome often does not reach to the inner plane of the layer. In the meristematic tissue the origin of the hair-cells, as short, dense wedge-shaped elements alternating regularly with longer and less dense cells, was ascertained. The atrichomic cell occasionally divides (as is shown in figure 70, plate 18).

These two cases show the presence in the Spadiciflorae of the phenomenon forming the chief topic of this paper.

Enantioblastae.

Representatives of three families of this group were studied: Commelinaceae, Eriocaulaceae, and Xyridaceae. The trichomes are of the specialized type.

Commelinaceae. Of *Tradescantia virginica* a growing rootlet showed trichoblasts as comparatively dense cells, two thirds as long as the alternate cells, at a distance of 0.3 mm. from the growing point, in tissue still covered by the cap. They were often lenticular. They had been cut, in the initiatory division, from the upper end of the mother cells. The bases of the mature trichomes are about one third the length of the atrichomic cells. *Commelina nudiflora*. Figure 71 (plate 18) gives in outline an optical longisection of the epidermis of one of the transparent rootlets. The first trichoblast appears as a proximal segment of the 12th cell from the apex. The division wall is straight. The trichoblastic segment is about one half as long as its congener. The next older and the remaining trichoblasts are rendered conspicuous by the density of their contents. Figure 73 (plate 18) shows these bodies in full face

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at the edge of the cap. *Commelina coelestis* also forms trichoblasts.

Eriocaulaceae. *Lachnocaulon Michauxii* is remarkable for its resemblance to Lycopodium in the longitudinal division of the trichoblasts, and the consequent occurrence of the root-hairs in groups of 2, 3, or 4 at the ends of the hairless epidermal cells. The trichoblasts first appear as distal segments, generally of lenticular form, often embracing less than the entire width of the cell-rows in which they are formed (pl. 18, fig. 74). They were seen to arise at about 40 cells from the apex in one actively growing root of considerable size. The trichoblasts divide longitudinally very shortly after formation. Commonly a single division suffices, but often this is followed by further division (pl. 18, fig. 75). Occasionally one of the half trichoblasts divides transversely (pl. 18, fig. 76). The inner part of the trichoblast spreads out, both transversely and longitudinally, jutting under the ends of contiguous atrichomic cells. In the fixed tissue the trichomes are sharply differentiated from the remaining elements by the extreme shortness as well as by the peculiar form of their bases (pl. 18, fig. 77). *Paepalanthus flavidulus* exhibits the same peculiarities. Trichoblasts were found which had undergone both transverse and longitudinal division, with the result that four trichomes were formed in a group. The trichoblasts originate as distal segments. This statement holds also for *Eriocaulon septangulare*. It is to be noted that as regards the origin of the trichoblasts, the Eriocaulaceae agree with the Glumiflorae, and that, as far as it goes, this evidence supports Engler's view that the Farinosae are derived from the Glumiflorae.

Xyridaceae. *Xyris flexuosa* var. *pusilla:* figure 79 (plate 18) represents a portion of the young fixed epidermal tissue, in which the distinction of trichomic and atrichomic cells is well seen. The hair emerges laterally as in several cases heretofore noted. Figure 78 (plate 18) shows a younger stage in profile. *Xyris caroliniana:* in figure 80 (plate 18) trichoblasts are seen in the region of increasing elongation of the root. The contrast between hair-cells and intervening prismatic cells is shown in figure 81 (plate 18).

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Liliiflorae.

In this group a single genus, Anigozanthos of the Haemodoraceae, was found to exhibit specialized hair-cells. In *Anigozanthos pulcherrima* (pl. 18, fig. 82–87; pl. 19, figs. 88, 89) the finer rootlets allow one to see the cells of the epidermis to the apex. At a distance of about 12 or 15 cells from the growing point the first fundaments of the trichomes may be seen (pl. 18, fig. 82). Tabular cells in this region are cut into unequal segments. The division walls are not inclined (pl. 18, fig. 83). The two segments of each mother cell stand to each other, as regards length, about in the ratio 2 : 1 or 3 : 2. The proximal segment is the shorter; this is the trichoblast. Very soon after its formation, it is seen to be richer in contents and darker colored than its atrichomic sister cell. The latter rapidly elongates, and in the roots examined, ultimately reaches an extension of 25 times its original length. On the other hand the trichoblast as a rule increases only 2 or 3 times in this dimension. The atrichomic cell was seldom found subdivided. In consequence the epidermis usually consists of two very dissimilar elements in regular alternation (pl. 19, fig. 88). Frequently the trichoblast divides longitudinally at an early stage (pl. 18, fig. 84), so that two collateral trichomes arise (pl. 18, fig. 87) as in Lachnocaulon, Luzula, and Lycopodium.

Scitamineae.

The following members of this family were examined, and I was able to assure myself that in each the trichomes are predetermined in the embryonic stage of the epidermis. The differentiation of the future hair-cells was in some cases only to be certainly determined from longisections of the root tip, although the distribution of the trichomes and their size — slightly less than that of other cells — was in these instances indicative of the mode of their formation. The nature of the hair-cells is most evident in Costus and Elettaria.

Musaceae: *Musa Cavendishiana.*

Zingeberaceae: *Costus* sp. (probably *spicatus*), *C. afer*, *Elettaria Cardamomum* (pl. 19, figs. 90, 91). In the last two species named the exact origin of the trichoblasts, as proximal segments in differentiating divisions of epidermal cells, was ascertained.

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Cannaceae: Canna × William Stone.
Marantaceae: *Maranta Leitzii* (pl. 19, fig. 92).

Gynandrae.

Among the few terrestrial orchids the roots of which were examined, the following have specialized hair cells: *Arethusa bulbosa* (pl. 19, fig. 96), *Calopogon pulchellus*, *Pogonia ophioglossoides* (pl. 19, fig. 93–95).

Nymphaeaceae.

A large number of Dicotyledons were studied, including many aquatic species. The Nymphaeaceae alone have trichomes predetermined in the formative region of the root tip. In species of Brasenia, Cabomba, Nuphar, and Nymphaea, the history of the root-hairs is like that of the same organs in the Monocotyledons which have been described above.

Nymphaea dentata (pl. 19, figs. 97–101). — The trichoblasts arise as narrow proximal segments in the transverse division of epidermal cells under the root-cap. These short cells have a high staining capacity, and are brought out strongly by the application of iodine. At the edge of the root-cap they are seen in longisection as granular cells with straight transverse walls, between the considerably elongated prismatic non-piliferous cells (pl. 19, fig. 97). The whole exterior wall is concerned in the outgrowth of the hair (pl. 19, fig. 100). The foot of the latter therefore covers the whole cell (pl. 19, fig. 101). The hairless cell becomes very long. The two kinds of cells alternate regularly.

The short cell may remain non-piliferous. In this event it may elongate somewhat and form a constituent of the epidermis differing from other cells only in length. Or it may become wedge-shaped, the edge outward, and by the pressing together of the adjacent cells in the row be pushed inward until the ends of the elongated cells meet above it and it no longer appears as a superficial element (pl. 19, fig. 97–99). This submergence of the trichoblasts was seen in *Nymphaea odorata* and *N. zanzibarensis* as well as in *N. dentata*. In addition to the species already named, the following were seen

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and agree with the above in essential respects: *N. amazonum* var. *blanda*, *N. coerulea*, *N. gracilis*, *N. rubra*, *N. scutellata*, *N. Smitheana*. *Nelumbium speciosum*, as I found it, had neither root hairs nor trichoblasts. *Brasenia peltata*, *Cabomba caroliniana*, and *Nuphar advena* (pl. 19, fig. 102) are much like Nymphaea.

Transfusion Cells of the Exoderm.

In the hypodermal layer, or exoderm of the root of many plants an alternation, in each longitudinal row, of elongated prismatic elements and short roundish or oval cells has been noted by several investigators.[1] As regards origin, form, and probable function, as well as distribution in Angiosperms, the short cells are related in an interesting way to the short trichomic elements of the epidermis already described. Several typical examples, which I have studied, may be briefly described.

Eucharis amazonica.— The alternation of long and short cells is established in the young exoderm, very near the growing point, by the unequal and slightly oblique division of the cells (pl. 19, fig. 103). The segmenting walls incline slightly toward the root apex as they run outward to the epidermis. The fundaments of the transfusion cells are therefore truncate wedge-shaped, the broader base outward. They are cut from the proximal end of the mother cells. Immediately afterwards they appear in the living state appreciably darker than the longer segments. As the layer matures, the smaller cells become rounded, as viewed tangentially. In radial longisection the general wedge-form is preserved. The outer face becomes strongly convex, and at the same time the adjacent long cells become curved in such a way as to elevate the short cells, which often protrude in a marked manner (pl. 19, fig. 104). The epidermis is thrown up into prominences. Its cells are sometimes separated above the protruding transfusion cells, which then have direct communication with the exterior. The transfusion cells often

[1] Oudemans: Ueber den sitz der oberhaut bei den luftwurzeln der orchideen. Verh. d. kon. akad. d. wetensch., Amsterdam, math. phys. klasse, **9** (1861).

Leitgeb: Die luftwurzeln der orchideen. Denkschr. d. akad. d. wiss., Wien, math. naturw. cl., **24** (1864).

Juel: Beitrage zur kenntniss der hautgewebe der wurzeln. Kongl. svenska vetenskaps-akad., Stockholm, Bihang t. handlingar, **9**, no. 9 (1884).

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become papillate (pl. 19, fig. 105), and thus in a manner, and to a slight degree, imitate the piliferous short cells of the epidermis of many plants.

Hyacinthus amethystinus.— The divisions giving rise to the transfusion cells were found to be oblique (pl. 19, fig. 106, T). The appearance of the cells in surface view is shown in figure 107 (plate 19) where it is clearly a proximal segment. In figure 108 (plate 19) a young transfusion cell is seen which has lately divided transversely, as trichoblasts divide in many instances (Juncus, Scirpus).

Pancratium ovatum.— The initiatory division is oblique. The proximal segment becomes the transfusion cell.

Aspidistra lurida.— In the material studied a dermatogen distinct from the root-cap and from the initials of the cortex, was found at the *punctum vegetationis*. In a certain section this dermatogen was observed, 7 cells from the apex, to split by periclinal walls into 2 layers, the outer of which became further divided to form a mantle of from 2 to 4 layers of short cells, while the inner became the hypodermal layer. In the hypodermal cell standing the 21st from the apex, an oblique transverse division wall had cut off a narrow proximal segment,— the rudiment of a transfusion cell (pl. 19, fig. 109, T). In the 22d cell the same thing had happened. In the 23d no division had taken place. In the 24th the transverse wall was nearly or quite perpendicular to the outer surface. In the fully developed exoderm the transfusion cells are short and rounded and project above the general surface of the layer (pl. 19, fig. 110). They are usually somewhat wedge-shaped in longisection. Figure 111 (plate 19) shows them in face view.

Anthericum Bernarnii.— The appearance of the alternating long and short cells is shown in figure 112 (plate 19).

Monstera deliciosa. — The short cells arise as proximal segments in divisions of hypodermal cells near the growing point.

Anthurium Scherzerianum. — The transfusion cells (pl. 19, figs. 113, 114) project above their companions. They are lenticular in tangential section, and are closely invested laterally by the more elongated cells. They are characterized by relatively abundant protoplasm.

Arundina bambusaefolia.— I have ascertained the origin of the transfusion cells. They arise as short proximal segments of the mother cells, and in a particular instance were noted at a distance of

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0.6 mm. from the apex. The mother cells were strongly convex, and the very short segments, cut from their extremities, were therefore at the beginning considerably inferior in breadth and height as well as in length, to their sister segments, the future elongated cells of the layer. The mature exoderm is shown in longisection in figure 115 (plate 19). Two short cells sometimes occur in succession. I have seen an instance in which this arrangement had just been established by the cutting off of a second segment taken from the proximal extremity of the longer daughter cell.

The genetic and structural resemblance of hypodermal short cells to trichoblasts is evident. The points of similarity in brief are these. Both short cells and trichoblasts arise as very short, often wedge-shaped segments. Both are often distinguished throughout life by relatively abundant granular protoplasm. De Bary says that the nucleus is often relatively large in the short hypodermal cells, as it often is in trichoblasts. Both hypodermal short cells and trichoblasts are apparently called into existence in response to stimulus. The production of transfusion cells is not a constant structural feature of the hypodermal layer, at least in many plants, in which I have noted that the formation of these cells may be intermitted on occasion, even over considerable areas of the hypoderm. In these cases it would seem that transfusion cells are formed in response to certain environmental conditions — a behavior typical of trichoblastic formation. This facultative character is apparent in many Liliiflorae. In the epiphytic Aroideae and Orchidaceae, the alternating structure has become more fixed.

There is also a functional similarity. Trichoblasts, or the trichomes into which they develop, are absorptive cells. The short cells of the exoderm have been termed *transfusion* cells, with probable reason. In many cases the arrangement or structure of neighboring elements — as for instance the pitted walls of overlying velamen cells (*Taeniophyllum Zollingeri* according to Müller) — and the thin membranes of the short cells, point to the short cells as gates in the hypodermal protective sheath, or integument. Müller says that in older, non-absorptive parts of the roots of *Taeniophyllum Zollingeri*, the short cells are stopped by the pressing down of overlying cells, the walls of which become thickened.[1]

[1] Müller, J.: Ueber die anatomie der assimilationswurzeln von *Taeniophyllum Zollingeri*. Sitzungsb. k. akad. d. wiss., Wien, math. naturw. cl., **109**, pt. 1 (1900).

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Oudemans demonstrated the distinctive chemical nature of the membranes of the short cells (Oudemans, *l. c.*). In sections treated with sulphuric acid and iodine, the elongated prismatic cells remained brown while the short cells stood out as alternating areas of blue, (cellulose reaction). Attention has been called above and in accompanying figures to the projection of the short cells. In *Eucharis amazonica* the communication of the short cells with the exterior is, in the older parts often direct.

The evidence from structure, therefore, indicates that the short cells of the exoderm have, in common with the short cells of the epidermis, an absorptive office.

The systematic distribution of the two phenomena under consideration is of interest. They are rarely found together (*Monstera deliciosa, Anigozanthos pulcherrima*). As will be seen from the list of species given below, special transfusion cells of the exoderm occur in those groups of the Monocotyledons which are without predetermined hair-cells. They are found also in many Dicotyledons.

These facts of anatomy, physiology, and distribution lead to speculation upon the morphological equivalence of the two sorts of cells. It may be surmised that they express the same original formative, structural principle. If the tegumentary structure prevailing in a large number of groups of Monocotyledons and in the higher vascular Cryptogams may be taken as the primitive condition, characteristic of the ancestry of the Monocotyledons, we may suppose that in the instances enumerated below (exclusive of the Dicotyledons) the tendency inherent in the epidermis to form trichoblasts has passed over to an underlying layer which histogenetically is closely related to the epidermis. This transference, it may be supposed, was effected in the modification of the tegumentary apparatus which we see in the groups in question, a modification necessitated by the epiphytic habit (Orchidaceae, Aroideae), or by life in the drier soils where periodic or occasional droughts are encountered (the majority of the Liliiflorae).

In the Monocotyledons the superficial layer of the young root (epidermis) is morphologically a cortical member. In Dicotyledons the epidermis has its origin in common with the root-cap; and the exoderm, therefore, the layer which in many Dicotyledons is characterized by the differentiation of transfusion cells — is the outer cortical layer, homologous with the external layer of the Monocoty-

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ledons. It is hence possible that the short exodermal cells of the Dicotyledons are strictly homologous with the trichoblastic elements of the epidermis of Monocotyledons. Assuming that both sorts of structure have had a common origin, the short hypodermal cells of the Dicotyledons may be regarded as potential trichomes, the trichomic development of which is prevented by the persistence of a sheath, the epidermis, derived from the root-cap. When this sheath fails, as in Nymphaea, the short cells then reveal their primitively trichomic character by resuming their proper development.

Whichever structure may have been the primitive one in the earliest Angiosperms, there seem to be grounds for regarding the differentiating process as one and the same whether it affects the epidermis or the exodermis.

The systematic distribution of transfusion cells of the exoderm. — Oudemans, Leitgeb, and De Bary observed a large number of cases in aerial roots of Aroideae and Orchidaceae. The list given below is that of Juel, augmented by instances which have come under my own observation. The latter are starred.

Liliaceae: *Agapanthus umbellatus, Allium narcissiflorum,* A. Schoenophrasum, Anthericum Bernarnii,* Arthopodium paniculatum, Brodiaea congesta,* Chlorophytum Sternbergianum, Dianella coerulea, D. stricta, Funckia lancifolia, F. ovata,* Hemerocallis fulva, Phormium tenax, Scilla peruviana, Veltheimia capensis, Xanthorrhoea arborea, Xerotes fluviatilis, X. longifolia, Yucca angustifolia, Y. Draconis.*

Convallariaceae: *Asparagus truophynus,* A. verticillatus, Convallaria majalis, C. multiflora, C. polygonatum, Cordyline stricta,* Dracaena cannaefolia, D. Draco, D. rubra, Maianthemum bifolium, Paris quadrifolia, Ruscus Hypoglossum, R. aculiatus, Semele androgyna, Smilacina stellata, Smilax herbacea.*

Amaryllidaceae: *Agave densiflora, Amaryllis amethystinus, A. Belladonna, A. vittata, Amorchis longifolia, Clivia miniata, C. nobilis, Crinum asiaticum, C. bracteatum, Doreanthus Palmeri, Eucharis amazonica, Galanthus nivalis, Haemanthus puniceus, Hymenocallis caribaea, Hypoxis erecta,* Narcissus poeticus, N. tazetta, Pancratium maritimum, P. ovatum,* Sprekelia formosissima, Vallota purpurea.*

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Iridaceae: *Sisyrinchium angustifolium.*
Araceae: *Acorus Calamus; Anthurium* and many other genera (Oudemans, Leitgeb).
Cannaceae: *Canna indica.*
Ranunculaceae: *Ranunculus bulbosus.*
Saxifragaceae: *Parnassia palustris.*
Haloragidaceae: *Myriophyllum ambiguum.**
Primulaceae: *Primula auricula, P. elatior, P. officinalis, Glaux maritima, Trientalis europaea, Lysimachia vulgaris, L. stricta.**
Scrophulariaceae: *Scrophularia nodosa, Gratiola officinalis.*
Labiatae: *Mimulus ringens.**
Gentianaceae: *Erythraea vulgaris, E. centaurium.*
Asclepiadaceae: *Hoya carnosa, Cynanchum vincetoxicum, Asclepias curassavica.*
Valerianaceae: *Valeriana officinalis.*

Concluding Remarks.

In the foregoing pages an interesting structure of the piliferous layer has been shown to be characteristic of most Pteridophytes above the ferns (it is found in a small group of the true ferns also) and of a large number of Monocotyledonous orders. In still other orders of Monocotyledons essentially the same structure is found, but occurs in an underlying layer. The question may be asked whether any inferences can be drawn as to the phylogenetic derivation of this structure, considered as a Monocotyledonous character.

The suggestion occurs that the structure under discussion may be merely adaptive and locally developed, in a systematic sense; that it is of no more systematic worth than such features as large intercellular spaces and reduction of stereome occurring in aquatic plants of various unrelated groups, or as multiplication of the epidermal layers of the root, characteristic of widely separated epiphytes; and that, in particular, the given structure may be due, in the plants in which it obtains, to the relation of the root to the presence of water. This view, however, seems not to be supported by the facts of distribution. Many of the species are hydrophytic, or at least semiaquatic; but perhaps as many others are mesophytic and not

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a few are more or less xerophytic. At the same time many aquatic plants, distributed amongst several of the larger groups of Monocotyledons and throughout the Dicotyledons, are without trichoblastic formations.

Granting that the character may have some phylogenetic significance, it is interesting to note that on the one side the peculiar structure of the piliferous layers so widely present in Monocotyledons is like that prevailing in the higher vascular Cryptogams; and that on the other side a structural resemblance may be traced to the outer cortical layer of the root in many Dicotyledons. In case the Angiosperms are from a Gymnospermous ancestry, the question which of the conditions found in the radical epidermis in the two divisions of the group is the original one, is one to which no answer can be given. The trichoblastic condition obtaining in Monocotyledons might be derived from that seen in Dicotyledons by denudation of the trunk proper, as in Nymphaea. At the present time, however, when the origin of flowering plants is obscure, it is pertinent to remark the dissimilarity of Angiospermae and Gymnospermae in respect to the organization of the apical region of the root, and, in contrast, the agreement of Angiospermae with certain Pteridophyta in this particular; and to call attention to the additional fact that the structure of the primary integument of the root-trunk obtaining so extensively in the branch of the Angiosperms, *viz.*, the Monocotyledons, which on the whole seems to be the more primitive, is closely similar to that prevailing amongst the higher Pteridophytes in the well marked feature which has been dwelt upon at length in this paper.

Many of the plants used in carrying out this research were seedlings. For seeds and in some instances for growing plants or preserved material I am greatly indebted to Sir W. T. Thiselton-Dyer, Prof. A. Engler, Prof. W. F. Ganong and Mr. E. J. Canning of Smith college, Mr. C. D. Beadle of Biltmore herbarium, Mrs. A. P. Taylor of Thomasville, Ga., Mr. Robert Cameron of the Harvard botanic garden, Dr. B. L. Robinson, and my associate, Mr. A. A. Eaton. The work has been made possible by the ample facilities of every kind provided by Mr. Oakes Ames.

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Explanation of Plates.

All figures were made by aid of the camera lucida. The arrow tip points in the direction of the apex of the root. The letter *e* attached to drawings of radial longitudinal sections indicates the external border of the section.

PLATE 16.

Fig. 1. *Aneimia adiantifolia.* Radial longisection of epidermal cells under the cap. The first trichoblast at T. × 410.

Fig. 2. *A. adiantifolia.* Rudiments of the trichomes immediately back of the cap. × 220.

Fig. 3. *A. adiantifolia.* Surface view of young trichomes. × 160.

Fig. 4. Longisection of the growing tip of a root of *Azolla filiculoides* (microtome section from material embedded in paraffin); T, trichoblast. × 450.

Fig. 5. *A. filiculoides.* Origin of the hair initials; close of mitosis and forming cell plate are seen at *d.* × 750.

Fig. 6. *A. filiculoides.* Trichoblasts and intervening cells at the beginning of the growth of the hairs, about ten cell pairs removed from the oldest shown in figure 4. × 450.

Fig. 7. *A. filiculoides.* First transverse division of intervening cell. × 450.

Fig. 8. *A. filiculoides.* Young root-hairs seen in tangential section of the root, showing zonal arrangement. × 450.

Fig. 9. *A. filiculoides.* Young hairs in radial longisection, separated in the row by four intervening cells. × 300.

Fig. 10. *A. filiculoides.* Base of mature hair, between elongated epidermal cells. × 450.

Fig. 11. Extremity of the root of *Azolla filiculoides.* × 5.[1]

Fig. 12. *Equisetum arvense.* Radial longisection of young epidermal cells, showing the origin of the trichoblast at T. The root-cap overlies these cells. × 410.

Fig. 13. *E. arvense.* Radial longisection of the epidermis a short distance from the root-cap. × 265.

Fig. 14. *E. arvense.* Tangential section of the epidermis before the emergence of the hairs. × 265.

Fig. 15. *E. arvense.* Young trichomes in longisection. × 265.

Fig. 16. *Lycopodium inundatum.* Radial longisection of cells lately divided for the formation of trichoblasts (T), lying under the root-cap. × 300.

Fig. 17. *L. inundatum.* Growth of the root-hairs. × 265.

[1] Figure 4–11 are here used by courtesy of the Botanical gazette.

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Fig. 18. *L. inundatum.* Bases of the trichomes in radial longisection. × 220.

Fig. 19. *L. inundatum.* Tangential section of epidermis, showing bases of the trichomes. × 220.

Fig. 20. *Lycopodium lucidulum.* Radial longisection of the epidermis showing the origin and development of the trichoblasts. T, the first trichoblast. × 410.

Fig. 21. *L. lucidulum.* Earliest stages of trichoblasts, seen tangentially. × 410.

Fig. 22. *L. lucidulum.* Longitudinal division of the trichoblast.

PLATE 17.

Fig. 23. *Isoetes canadensis.* Superficial view of the young epidermis, in the region of the formation of trichoblasts, beginning with the 25th cell (*c*) from the apex of the root. The trichoblasts (T, T, *etc.*) are distinguished by relatively dense contents. × 410.

Fig. 24. *I. canadensis.* The trichoblast and three atrichomic cells of the same group, in longisection. × 410.

Fig. 25. *I. Engelmanni.* Trichomic and atrichomic cells in longisection in the region in which the hairs begin to appear. × 240.

Fig. 26. *Isoetes* sp. Young elongating epidermis at the edge of the root-cap, in superficial view. × 260.

Fig. 27. *I. foveolata.* Superficial aspect of the mature epidermis. × 220.

Fig. 28. *Selaginella rupestris.* Optical longisection of the epidermis at the edge of the cap. T, the first trichoblastic segment. × 410.

Fig. 29. *S. rupestris.* Bases of trichomes. × 260.

Fig. 30. *S. denticulata.* Part of an epidermal cell row in surface view. × 260.

Fig. 31. *Limnocharis emarginata.* Longisection of the epidermis beginning with the 18th cell from the apex. The first trichoblastic division at T; *b* continues *a* with a slight break. × 260.

Fig. 32. *L. emarginata.* Trichoblasts in tangential section, before the appearance of root-hairs. × 260.

Fig. 33. *L. emarginata.* Lower part of mature trichome. × 260.

Fig. 34. *Triglochin maritima.* Base of trichome. × 490.

Fig. 35. *Ruppia maritima.* Base of trichome. × 490.

Fig. 36. *Zannichellia palustris.* Base of trichome. × 490.

Fig. 37. *Naias gracillima.* Tangential section of epidermis, showing lately formed trichoblasts (as at T). × 410.

Fig. 38. *N. gracillima.* Longisection of epidermis near the edge of the cap. × 315.

Fig. 39. *N. gracillima.* Development of the root-hairs. × 315.

Fig. 40. *N. gracillima.* Superficial view of the epidermal cells immediately back of the root-cap. T, the young trichome. × 220.

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Fig. 41. *Naias flexilis.* Superficial appearance of the base of the trichome. × 315.
Fig. 42. *N. flexilis.* Side view of the base of the trichome. × 315.
Fig. 43. *Sagittaria Eatoni.* Surface of the epidermis near the apex of the root, showing the youngest stages of the trichoblast (as at T). × 220.
Fig. 44. *S. Eatoni.* Radial longisection of epidermis showing the origin of the trichoblast (T). × 300.
Fig. 45. *S. subulata.* Trichoblasts and atrichomic cells in radial longisection slightly stained with iodine. × 260.
Fig. 46. *S. subulata.* Trichome. × 260.
Fig. 47. *S. lancifolia.* Surface of the epidermis, 0.4 mm. from the growing point. × 260.
Fig. 48. *S. lancifolia.* Base of trichome in profile. × 260.
Fig. 49. *Limnobium spongia.* Optical radial longisection of living epidermis. T, trichoblast. × 160.
Fig. 50. *L. Spongia.* Superficial view of the same. T, trichoblast. × 160.
Fig. 51. *L. Spongia.* Young trichome. × 560.
Fig. 52. *Juncus arcticus.* Origin of the trichoblasts. Superficial view of the epidermis near the apex. T, trichoblasts. × 410.
Fig. 53. *J. acuminatus.* Trichoblast and intervening cells in profile, 0.3 mm. from the growing point. Division at *d.* × 300.
Fig. 54. *Luzula sudetica.* Surface of epidermis very near root tip. Lately formed trichomic cells (as at T). × 410.
Fig. 55. *L. campestris.* Divisions of the trichoblasts. Superficial view of the young epidermis. × 410.
Fig. 56. *L. comosa.* Base of mature trichome. The second trichome of the pair is shown in broken line. × 220.

PLATE 18.

Fig. 57. *Cyperus rivularis.* Optical longisection of parts of a rootlet. The first trichoblast at T. Trichomic cells are distinguished by dense contents. × 300.
Fig. 58. *C. alternifolius.* Trichomes and non-piliferous cells in profile.
Fig. 59. *C. alternifolius.* Trichoblasts in profile, 0.5 mm. from the apex. × 300.
Fig. 60. *Carex crinita.* Alternation of short and long (trichomic and atrichomic) cells in the young epidermis. × 315.
Fig. 61. *C. crinita.* Young trichome and hairless cells in profile. × 315.
Fig. 62. *Rhynchospora fusca.* Surface of the root, 1 mm. from the apex, showing trichoblasts. × 300.
Fig. 63. *Scirpus maritimus.* Profile of epidermal cells below the region of root-hairs. Trichoblasts distinguished by contents and by color of walls. × 300.
Fig. 64. *S. maritimus.* Base of trichome and elongated non-piliferous cell in longisection. × 300.

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Fig. 65. *Alopecurus occidentalis.* Optical radial longisection of epidermal cells about 30 cells from the growing point. × 315.

Fig. 66. *A. occidentalis.* Trichoblasts (T, T) and hairless cells 0.1 mm. from the growing point. Radial longisection. × 315.

Fig. 67. *A. occidentalis.* Base of trichome and atrichomic cells in profile. × 315.

Fig. 68. *Festuca arundinacea.* Surface view of part of a cell row in the embryonic epidermis. Alternation of trichoblasts (T) and non-piliferous cells. × 300.

Fig. 69. *Poa violacea.* Base of trichome and fully elongated hairless cell, in profile. × 315.

Fig. 70. *Monstera deliciosa.* Young root-hairs in alternation with hairless elements, in profile. × 220.

Fig. 71. *Commelina nudiflora.* Optical longisection of epidermis and cap of a small rootlet. The first trichoblast at T. × 450.

Fig. 72. *C. nudiflora.* The epidermis immediately back of that represented in figure 71. × 450.

Fig. 73. *C. nudiflora.* Surface of the epidermis just back of the root-cap. × 450.

Fig. 74. *Lachnocaulon Michauxii.* Superficial view of the epidermis near the growing point, about 40 cells from the apex. × 220.

Fig. 75. *L. Michauxii.* Young trichomes in surface view. × 220.

Fig. 76. *L. Michauxii.* Trichomes in surface view. × 220.

Fig. 77. *L. Michauxii.* Young trichome in radial section. × 420.

Fig. 78. *Xyris flexuosa* var. *pusilla.* Trichoblasts and long cells in profile, in the younger fixed tissue, below the root-hairs. × 300.

Fig. 79. *X. flexuosa* var. *pusilla.* Surface of the root 2 mm. from the apex. Young trichomes, the hairs emerging laterally. × 300.

Fig. 80. *X. caroliniana.* Surface of two cell rows 0.25 mm. from the apex. The trichoblasts occasionally transversely divided, as at *d.* × 300.

Fig. 81. *X. caroliniana.* Oblique view of the surface of the root in the zone of young hairs. × 220.

Fig. 82. *Anigozanthos pulcherrima.* Part of a longitudinal cell row of the epidermis, beginning with the 12th cell from the apex, in superficial view. The first trichoblast at T. × 300.

Fig. 83. *A. pulcherrima.* Epidermal cells divided for the formation of trichoblasts (as at T), in profile. × 300.

Fig. 84. *A. pulcherrima.* Surface of the epidermis at about the limit of the cap. × 300.

Fig. 85. *A. pulcherrima.* Trichoblast formed by the cutting off of one corner of the mother cell. × 300.

Fig. 86. *A pulcherrima.* Lateral position of the hairs. × 220.

Fig. 87. *A. pulcherrima.* Bases of a pair of trichomes. × 300.

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PLATE 19.

Fig. 88. *Anigozanthos pulcherrima.* Extremity of a rootlet. × 300.

Fig. 89. *A. pulcherrima.* A part of the epidermis after the appearance of the hairs. × 220.

Fig. 90. *Elettaria Cardamomum.* Trichomic and intervening cells in profile, at the beginning of the growth of the hairs. × 315.

Fig. 91. *E. Cardamomum.* Trichomes and hairless cells in alternation. × 315.

Fig. 92. *Maranta Leitzii.* Superficial view of the mature epidermis. × 315.

Fig. 93. *Pogonia ophioglossoides.* Trichoblast and hairless cells in profile, 6 mm. from the apex of a rapidly growing root.

Fig. 94. *P. ophioglossoides.* Base of trichome between elongated cells, in profile.

Fig. 95. *P. ophioglossoides.* Superficial view of the epidermis showing the trichome.

Fig. 96. *Arethusa bulbosa.* Young trichomes in surface view. × 220.

Fig. 97. *Nymphaea dentata.* Radial longisection of the epidermis at the border of the root-cap. × 450.

Fig. 98. *N. dentata.* Epidermal cells in profile, 5 cells back from those represented in figure 97. × 450.

Fig. 99. *N. dentata.* Superficial appearance of the cells represented in figure 98. × 450.

Fig. 100. *N. dentata.* Young trichome. × 450.

Fig. 101. *N. dentata.* Partly grown trichome. × 220.

Fig. 102. *Nuphar advena.* Surface of the epidermis below the zone of root-hairs.

Fig. 103. *Eucharis amazonica.* Radial longisection through cap, epidermis, and exoderm, showing the origin of the exodermal transfusion cells. × 220.

Fig. 104. *E. amazonica.* Transfusion cell of mature exoderm in profile. × 160.

Fig. 105. *E. amazonica.* Transfusion cell in older exoderm, above which the epidermal cells have separated.

Fig. 106. *Hyacinthus amethystinus.* Optical radial longisection of epidermis and exoderm at the edge of the cap, showing the origin of the transfusion cells (as at T). × 410.

Fig. 107. *H. amethystinus.* Superficial view of the cells shown in figure 106. × 410.

Fig. 108. *H. amethystinus.* Exodermal transfusion cells at a later stage, in profile. × 410.

Fig. 109. *Aspidistra lurida.* Radial longisection of the exoderm beginning with the 31st cell from the apex. The first transfusion cell at T. × 300.

Fig. 110. *A. lurida.* Longisection of sheath and exoderm, showing alternation of long and short cells in the exoderm, 8 mm. from the apex. × 300.

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Fig. 111. *Aspidistra lurida.* Tangential section showing the exoderm. × 220.

Fig. 112. *Anthericum Bernarnii.* Epidermis and exoderm in profile, 3 mm. from the apex. × 315.

Fig. 113. *Anthurium Scherzerianum.* Radial longisection of epidermis and exoderm. 300.

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Fig. 115. *Arundina bambusaefolia.* Radial longisection of velamen and exoderm.

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